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Citation style: Chmura Damian, Tokarska-Guzik Barbara, Nowak Teresa, Woźniak Gabriela, Bzdęga Katarzyna, Koszela Katarzyna, Gancarek Małgorzata. (2015). The influence of invasive Fallopia taxa on resident plant species in two river valleys(southern Poland). " Acta Societatis Botanicorum Poloniae" (Vol. 84, iss. 1 (2015), s. 23-33), doi 10.5586/asbp.2015.008

Acta Societatis Botanicorum Poloniae

ORIGINAL RESEARCH PAPER Acta Soc Bot Pol 84(1):23–33 DOI: 10.5586/asbp.2015.008
Received: 2014-03-14 Accepted: 2015-02-18 Published electronically: 2015-03-16

The influence of invasive *Fallopia* taxa on resident plant species in two river valleys (southern Poland)

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Abstract

Riparian zones in two rivers in southern Poland were studied in terms of species composition and soil parameters in patches dominated by three knotweed taxa (*Fallopia japonica*, *F. sachalinensis* and the hybrid *F.* ×*bohemica*). The main purpose was to detect any differences in species diversity, environmental conditions and in the impact of the three *Fallopia* spp. on resident species. Fieldwork was conducted in spring and summer in 30 invaded plots (in total 90 subplots). It was demonstrated that vegetation dominated by particular knotweed taxa differed in response to soil pH and ammonium, nitrate, and magnesium content. *Fallopia* spp. (living plants and necromass) had a stronger negative impact on the cover and species diversity of the resident species in summer in comparison with spring. Vegetation patches differed significantly in species composition in relation to the knotweed taxa present. These differences may be the consequence of the differentiated biotopic requirements of *Fallopia* taxa and the coexisting plants, or to the different impact of the knotweed taxa on the resident species.

Keywords: biological invasions; *Reynoutria* taxa; riverside vegetation; phenology

Introduction

Species diversity remains one of the significant criteria investigated in contemporary ecology, being considered a suitable measure of the quality of the environment ([1] and the literature cited therein). At the same time invasion by alien species has been recognized as one of the major threats to natural biodiversity [2], although individual habitats vary considerably in their susceptibility to invasion [3].

Riparian woodlands are communities with high species richness, identified as habitats with especial nature conservation value (e.g. [4,5]). These particular habitats, together with other waterside situations, are the most endangered by and most easily invaded by alien invasive plants [6,7], and then play a role of transmission into other more typically terrestrial habitats, such as dry scrub and woodland. This fact has an important role in planning management for river banks and river valleys.

Among the world's most invasive vascular plants are the representatives of the genus *Fallopia* (syn. *Reynoutria*; Polygonaceae): *F. japonica* (Houtt.) Ronse Decraense, *F. sachalinensis* (F.W. Schmidt ex Maxim.) Nakai, and the hybrid *F.* ×*bohemica* (Chrtek and Chrtková) J. Bailey (e.g. [8]). This *Fallopia* species complex, sometimes referred to as Japanese knotweed sensu lato, penetrates both into plant communities transformed by humans, and into natural communities, including those of alluvial plains (e.g. [9–14]), and the taxa are simultaneously a remarkable example of transformer species [15].

Fallopia taxa are among the tallest polycarpic perennial plants. They have aerial annual stems up to 3–4 meters high, and are able to form very dense monospecific patches [12,16]. Their rhizome system is very dense and can grow to 2 meters in depth [17]. Recent studies have shown that, apart from extensive vegetative growth, hybridization between the *F. japonica* and *F. sachalinensis* has created even more highly invasive genotypes of the hybrid *F.* ×*bohemica* that are able to establish themselves by seed [15,18,19].

The stand-forming habit of these species produces a dense summer canopy beneath which few other species can survive due to competition for light [14,20,21]. In addition, their rhizome system grows rampantly, producing stem litter, and the plants intensively remove nutrients from the soil, thus also taking over ground from their competitors ([12,22,23] and the literature cited therein). The same authors

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Handling Editor: Zygmunt Dajdok

conclude that *Fallopia* taxa (*F. japonica*) may contribute to soil homogenization in invaded landscapes.

All these factors, together with changes in the abiotic or biotic environment in *Fallopia* populations, may also affect the germination and survival of seedlings or juvenile plants of native species, and thus prevent their colonization and recruitment [24]. Other authors point out that allelopathy may play a role in the impact of *Fallopia* invasion on the species diversity of invaded communities [14,25].

Invasion success in alien species is dependent on a set of many plant traits which make it more invasive. Differences in the biology of the studied *Fallopia* taxa may result in differences in the way they affect the riparian vegetation patches in which they occur [26]. In the riparian habitats the participation of *F. japonica*, *F. sachalinensis* and their hybrid *F. ×bohemica* varies in the number and abundance of the different taxa [20].

Previous studies confirming the possibility of the sexual reproduction (also, indirectly, through the genetic variability found in *F. ×bohemica*), showed that the *Fallopia* species differ in their ecology, establishment success [27,28], response to control measures [28], genetic variation [29], and their effect on the germination and establishment of species in invaded stands [14]. A few previous studies suggested that three *Fallopia* taxa differed in their competitive ability. Hybrid *F. ×bohemica* was proven to spread faster, and this is also possibly due to its genetic diversity. A study using experimental communities of native plants and *Fallopia* taxa revealed that the hybrid performed significantly better than the parental species [30]. Some studies on other species showed that hybrids can be more plastic and more tolerant to environmental conditions [31].

Even though the invasion by *Fallopia* taxa is among the most intensively studied phenomena globally [14,32,33], nevertheless new aspects should be paid attention to and need explanation. More rarely undertaken studies, determining the influence of *Fallopia* taxa on abiotic and biotic conditions of particular habitats, devote attention to individual taxa from the *Fallopia* genus. One example of such a study, although limited to laboratory conditions, was the experiment designed by Moravcová et al. [14], showing that *Fallopia* above-ground plant parts could potentially inhibit the germination of other plant species, and that the effect differs among the three taxa of the genus.

Records of *Fallopia* taxa occurring in riparian vegetation patches are numerous, but the exact influence of soil properties on their presence, and the impact of knotweeds on the species composition of invaded sites have not been studied in detail. Previous studies have revealed that all three *Fallopia* congeners separately exhibit a negative impact on species richness and species composition in sites which they invade [34]. A few studies (e.g. [19]) analyzed the species composition of sites invaded by *Fallopia* but by using phytosociological relevés, without environmental measurements and on a small number of plots.

One of the most important aspects of the project presented here is to assess the effect of particular *Fallopia* taxon on species diversity. We seek to determine which soil parameters affect the species composition of vegetation patches dominated by *Fallopia* taxa. We are interested in how strong, and if any, is the negative impact of cover of particular *Fallopia* taxa on species diversity, and how it varies during the vegetation season. We would like to know whether there are differences among *Fallopia* taxa regarding this aspect in terms of season and the whole year. The other important issue is the influence of the necromass forming due to the decomposition of fallen leaves from *Fallopia* plants. The role of the cover of mosses and its relation with vascular plants including *Fallopia* taxa is also highlighted.

Based on the aforementioned questions the following hypotheses were formulated with the intention of falsifying them:

(***i***) The patches of riparian vegetation dominated by *Fallopia* spp. do not differentiate equally along environmental gradients. We expected that *F. ×bohemica* patches would show the highest variation and *F. sachalinensis* show the lowest.

(***ii***) There are no differences in the biotopic requirements of *Fallopia* patches between spring and summer.

(***iii***) The cover of *Fallopia* taxa in summer is higher than in spring, whereas the total cover of resident species, both vascular and moss species, is lower due to the impact of knotweeds.

(***iv***) The species diversity of native plants under the canopy of *Fallopia* spp., measured by various biodiversity indices, decreases during the vegetation season what is mainly caused by phenology but can be modified by impact of knotweeds.

Material and methods

Data collection

For the purposes of the present study data were collected from riparian vegetation patches invaded by the three *Fallopia* taxa, occurring along two river valleys in southern Poland: the valleys of the Biała and Jasienica rivers (Fig. 1a). Along the rivers examined, vegetation consists of a mosaic of long-established semi-natural communities and intermediate to highly disturbed sites surrounded by agricultural fields. Permanent plots were set up in riparian vegetation patches in which the taxa studied: *F. japonica*, *F. ×bohemica* and *F. sachalinensis* had become the dominants in the herb layer.

In total, 30 invaded plots (90 subplots) were set up in riparian communities along the two aforementioned river valleys (15 plots in each valley) as presented in the scheme (Fig. 1b). The plots were selected according to the following criteria: (***i***) the site was heavily invaded by the objective *Fallopia* taxa individuals, with its populations as spatially homogeneous as possible, (***ii***) the invaded sites were adjacent to uninvaded riparian vegetation, (***iii***) the sites invaded by the three studied *Fallopia* taxa were as close as possible to get habitat conditions as unified as possible.

The experimental plots were established with the following design: (***i***) homogeneous *F. japonica* populations in five replicates along the Jasienica, and ten replicates along the Biała river; (***ii***) five plots with *F. ×bohemica* along the Jasienica and five along the Biała river; (***iii***) five plots with *F. sachalinensis* but only in the Jasienica river valley because along the Biała river *F. sachalinensis* patches were absent.

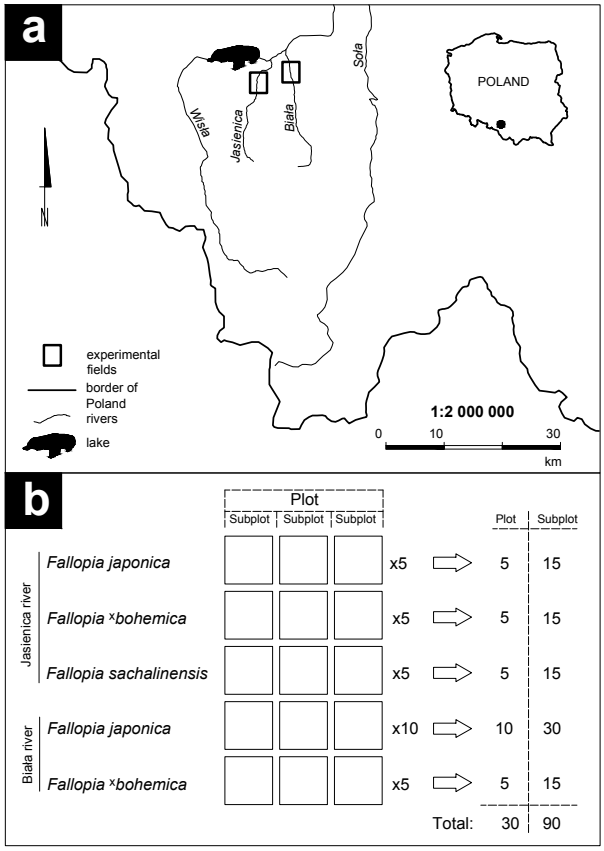

Fig. 1 Situation of the study area and sampling design.

Each plot (10 × 4 m) was divided into three smaller subplots of 2 × 2 m with a distance of 1 meter and 1 meter of border. For each subplot the cover of above-ground parts of all vascular plants present was recorded using 1, 2, 5% and further 10% intervals. The cover of the moss layer and the cover of decaying biomass (litterfall), referred to here as necromass, were also estimated. These field measurements were made in late April (spring) and at the beginning of July (summer). No uninvaded sites were subjected to these studies.

Data on site abiotic conditions were collected in the same subplots (Tab. 1). In each subplot five soil cores (0–10 cm depth, litter discarded) were taken with a soil borer (4 cm in diameter) – one core was sampled at each corner of the square and one core at the center of the square. These five cores were mixed into a single bulk sample for each plot. Soil samples were air-dried to a constant weight and sieved (<2 mm). The following parameters were assessed on each sample: soil pH, extractable potassium, available magnesium (the Schatschabel method), total phosphorus and total carbon (the calorimetric and the Tiurin method, respectively), the extractable ammonium nitrogen N-NH_4 and total nitrate nitrogen content.

Statistical analysis

In order to examine which species are significantly associated with, i.e. they can be interpreted as species best adopted or survived in vegetation patches invaded by knotweeds, one or two of the three *Fallopia* taxa studied, the IndVal (indicator value analysis) method was applied. The IndVal quantifies the fidelity and specificity of species in relation to groups of sites in a user-specified classification of sites and tests for the statistical significance of the associations ([35] and literature cited therein). Vegetation patches dominated by knotweeds except for *F. sachalinensis* were present in both river valleys so there was a high possibility of finding the same native plant species in each already mentioned plot. The classification of co-occurring species into three groups of sites – invaded by particular *Fallopia* taxa – at the scale of subplot and in a further step in the combination of the two groups of sites was performed. The statistical significance of this relationship was tested using a test with 999 permutations.

On the basis of plants present the following biodiversity indices were calculated: Shannon–Wiener index H', Simpson diversity index D', evenness E and species richness S. The presence and cover of *Fallopia* taxa were excluded from the calculations. The Wilcoxon paired test was employed to assess the significance of changes between spring and summer in the cover of *Fallopia* taxa, total cover of vascular plants, cover of the moss layer, and mean values of biodiversity indices. To examine the relationships between biodiversity indices and total cover of *Fallopia* taxa, the Spearman rank correlation was made for two parts (spring and summer) of the growing season separately. Furthermore, data from spring and summer was combined in another analysis. For the same plots maximum cover of all plants present in subplots were compared. The canonical correspondence analysis (CCA) method with a matrix of soil parameters and species cover including knotweeds was used to show how patches with *Fallopia* taxa are distributed along environmental gradients. To study how the cover of particular taxa of the *Fallopia* genus, as well as necromass and moss cover, affect the species composition of the vascular flora of riparian habitats, CCA was also carried out. In both cases the CCA method was conducted with log transformation of data and with the Monte Carlo test (999 permutations) using CANOCO software (http://www.microcomputerpower.com). The CCAs were performed separately for spring and summer. Other statistical tests were performed using R software (http://www.r-project.org).

Tab. 1 Descriptive statistics (median ±interquartile range) of soil parameters of the river valleys of the Biała and the Jasienica.

Parameter	Biała	Jasienica
pH	6.53 ±1.6	6.51 ±1.3
Total P_2O_5 (mg 100 g^{-1})	14.0 ±5.8***	6.5 ±6.0
Extractable K_2O (mg 100 g^{-1})	16.9 ±18.2	22.5 ±15.6
Available Mg (mg 100 g^{-1})	11.4 ±10.9	9.7 ±5.6
Total C org (%)	2.5 ±1.7	2.2 ±0.7
N-NO_3 (mg/kg dry mass)	3.95 ±2.09	5.43 ±5.79
N-NH_4 (mg/kg dry mass)	6.48 ±4.36	12.96 ±9.00***

*** $P < 0.001$.

Results

Both river valleys were similar in terms of chemical parameters except for soil phosphorus content, which was higher along the Biała river, and concentrations of ammonium ions which were higher along the Jasienica river (Tab. 1).

In spring, pH, magnesium, and nitrogen (nitrates, ammonium ions) significantly explained influenced the species composition of patches with *Fallopia* taxa (Tab. 2). The vegetation patches with *F. japonica* were largely confined to higher pH, patches with *F.* ×*bohemica* to higher contents of magnesium and potassium, whereas patches with *F. achalinensis* were characterized by a higher content of nitrogen (Fig. 2). In summer the situation was very similar. However, organic carbon started to play a more significant role for some sites with *F.* ×*bohemica* (Tab. 2, Fig. 3). Both analyses demonstrated that vegetation patches dominated by *F. japonica* and *F.* ×*bohemica* overlap more than those of *F. sachalinensis* in spring, whereas in summer all three types of plots differed significantly in terms of relationships with to soil variables. The Kruskal–Wallis test, followed by Conover test, revealed significant difference in the mean values of plot coordinates along the first two axes of CCA constrained by the used environmental variables in spring (Axis 1, $\chi^2 = 25.4$, $P < 0.0001$; Axis 2, $\chi^2 = 10.7$, $P < 0.004$) and summer (Axis 1, $\chi^2 = 32.4$; $P < 0.0001$; Axis 2, $\chi^2 = 39.7$, $P < 0.001$).

Tab. 2 The results of the Monte Carlo test (*P*-values) in CCA with soil parameters as constraining variables.

Parameter	Spring	Summer
Mg	**0.001**	**0.001**
pH (KCl)	**0.002**	**0.001**
Ammonium (N-NH_4)	**0.035**	**0.001**
Nitrate (N-NO_3)	**0.008**	**0.032**
K (K_2O)	0.098	0.278
C org	0.351	**0.035**
P (P_2O_5)	0.303	0.062

Bold values are significant at $P < 0.05$.

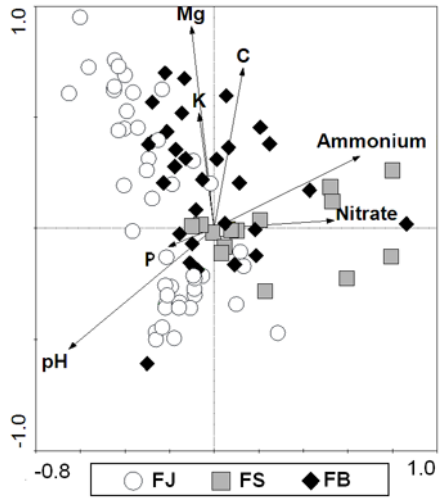

Fig. 2 Ordination of vegetation plots with *Fallopia* taxa and soils (data for spring) along the first two CCA axes ($\lambda_1 = 0.32$, $\lambda_2 = 0.28$). The diagram accounts for 7.6% and 53.6% of variance of cover species data and fitted species data, respectively. FJ – *F. japonica*, FS – *F. sachalinensis*, FB – *F.* ×*bohemica*.

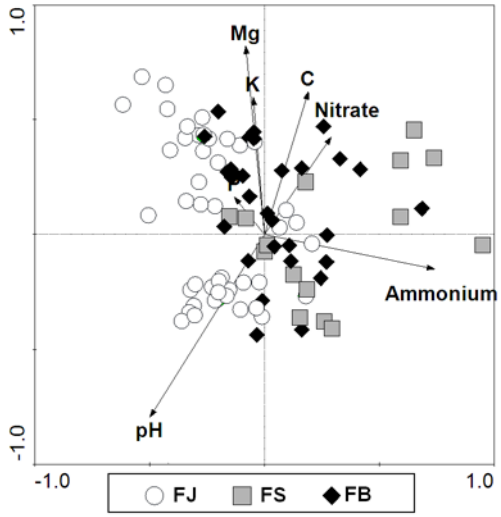

Fig. 3 Ordination of vegetation plots with *Fallopia* taxa and soils (data for summer) along the first two CCA axes ($\lambda_1 = 0.42$, $\lambda_2 = 0.25$). The diagram accounts for 9.7% and 54.4% of variance of cover species data and fitted species data, respectively. FJ – *F. japonica*, FS – *F. sachalinensis*, FB – *F.* ×*bohemica*.

Analysis of the abundance of plants during the two seasons demonstrated that in summer the total cover of *Fallopia* taxa was ca. tenfold higher, whereas the cover of all native plants was slightly higher. The cover of mosses did not change significantly, but in turn the cover of necromass decreased (Fig. 4a–c). The biodiversity indices as the mean number of species (Fig. 4d), mean value of Shannon–Wiener (Fig. 4e) and Simpson index (Fig. 4f) were higher in spring than in summer. Only evennes did not change significantly (Fig. 4g).

As shown, the total cover of *Fallopia* spp. had a negative impact on biodiversity, especially in summer. In spring *Fallopia* taxa only negatively influenced the number of species, but in summer they also affected the dominant species as well as the total cover of resident species (Tab. 3). Necromass in spring was negatively correlated, but in summer there was a positive relationship with the total cover of knotweeds. Analysis of vegetation patches dominated by particular taxa in both seasons demonstrated differences among knotweeds. Surprisingly the dominance of *F. sachalinensis* was positively correlated with species richness likewise with the Shannon–Wiener index and moss cover using the data for the whole year. Necromass, however, was negatively correlated with cover of *F. sachalinensis* both in spring and in summer. The data for spring and summer combined revealed negative

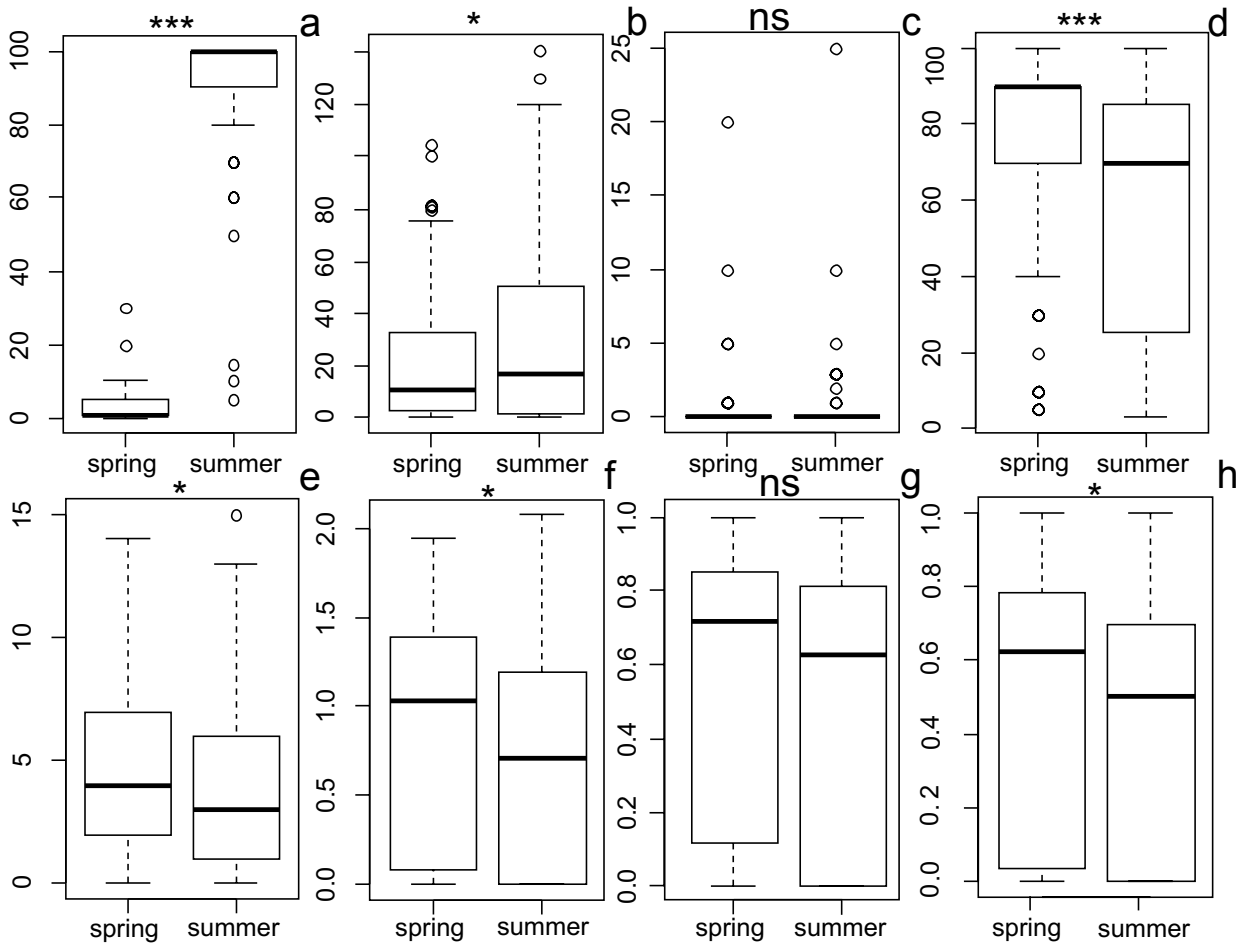

Fig. 4 Comparison of cover of *Fallopia* spp. (**a**), cover of native species (**b**), cover of mosses (**c**), cover of necromass (**d**), values of species richness (**e**), Shannon–Wiener (**f**), evenness (**g**), Simpson index (**h**) between spring and summer. * $P < 0.05$; *** $P < 0.001$; ns – non-significant (Wilcoxon paired test).

Tab. 3 The Spearman rank correlation coefficients between cover of *Fallopia* taxa combined and particular *Fallopia* taxa and biodiversity indices, necromass and total cover of native species for spring and autumn and whole year combined.

	***Fallopia* taxa combined**			***F. japonica***			***F. sachalinensis***			***F. ×bohemica***		
Parameter	**Spring**	**Summer**	**Combined**	**Spring**	**Summer**	**Combined**	**Spring**	**Summer**	**Combined**	**Spring**	**Summer**	**Combined**
H'	ns	**−0.43*****	ns	ns	ns	ns	ns	ns	0.21*	ns	ns	−0.21*
D	ns	**−0.30*****	ns	ns	ns	ns	ns	ns	ns	ns	ns	−0.29**
E	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
S	0.22*	**−0.54*****	**−0.31****	ns	ns	ns	ns	ns	**0.22***	ns	ns	−0.27*
Moss cover	0.25*	ns	ns	ns	ns	ns	**0.48*****	**0.34****	**0.34****	ns	ns	ns
Necromass	**−0.44***	**0.41*****	ns	ns	**0.31*****	0.31	**−0.51*****	**−0.34****	**−0.34****	ns	ns	ns
Total cover of natives	ns	**−0.57*****	**−0.43*****	ns	**−0.35*****	−0.32	0.24*	ns	ns	ns	ns	ns

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns – non-significant. Bold values are significant after Bonferroni–Holm correction for multiple tests.

correlations between some biodiversity indices in patches dominated by the hybrid *F. ×bohemica*. In turn Japanese Knotweed (*F. japonica*) cover was negatively correlated with total cover of native plants over the year and positively with necromass.

The Monte Carlo test showed that necromass had a significant correlation with species composition in spring, and the cover of mosses also significantly explained this variable (Tab. 4). A weak influence of *F. ×bohemica* cover was also recorded (Fig. 5). In summer the situation changed.

Tab. 4 The results of the Monte Carlo test (*P*-values) in CCA with cover of *Fallopia* taxa, necromass and moss cover as constraining variables.

Parameter	Spring	Summer
Necromass	**0.001**	**0.001**
Moss cover	**0.046**	0.387
Fallopia ×bohemica	**0.050**	**0.001**
Fallopia sachalinensis	0.096	**0.004**
Fallopia japonica	0.690	**0.044**

Bold values are significant at $P < 0.05$.

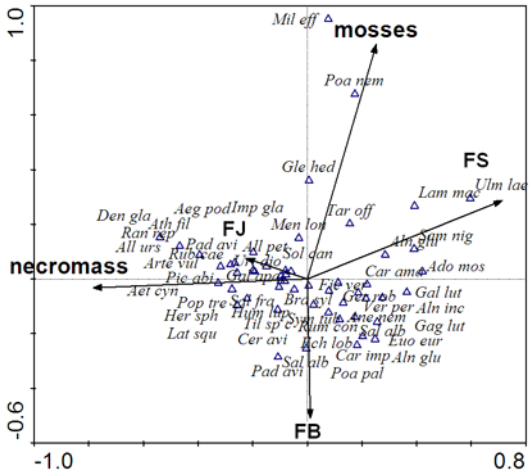

Fig. 5 Biplot of field layer species and *Fallopia* taxa (FJ, FS, FB), cover of mosses and necromass as predictor variables on the first two CCA axes ($\lambda_1 = 0.33$, $\lambda_2 = 0.27$) in spring. The diagram accounts for 6.7% and 62.0% of variance of cover species data and fitted species data, respectively. The first three letters indicate the genus and species names, respectively.

In summer the species composition was mostly correlated with the presence of necromass, and the cover-abundance of all *Fallopia* taxa. *Fallopia* japonica affected the species composition less than the two other taxa. No influence of moss cover was recorded (Fig. 6).

Species which coexisted most frequently with particular *Fallopia* taxa, are listed in Tab. 5 and Tab. 6. With *F. japonica*, the most frequent species both in spring and summer were: *Phalaris arundinacea* L. and *Agrostis capillaris* L. whereas, only in spring, mainly *Urtica dioica* L. and *Impatiens glandulifera* Royle. Sites invaded by *F. ×bohemica* were also sites of the occurrence of *Populus tremula* L. as trees and seedlings (Tab. 5, Tab. 6). Other frequent but not significantly associated species were: *Poa palustris* L., *Cardamine impatiens* L., and seedlings of *Cerasus avium* L.(Moench). The species which co-occurred with *F. sachalinensis* were *Poa nemoralis* L., *Agrostis capillaris*, *Adoxa moschatellina* L., *Cardamine amara* L.s.s., and trees of *Alnus incana* L. (Moench) and *Ulmus laevis* Pall. Some species, such as *Alliaria petiolata* (M. Bieb.) Cavara & Grande and *Ficaria verna* Huds. in spring, and *Glechoma hederacea* L. in summer, are equally confined both to *F. japonica* and *F. sachalinensis* stands. Trees of *Salix alba* L. were significantly more frequent in stands of *F. sachalinensis* and *F. ×bohemica* (Tab. 5, Tab. 6). No common associated species for both *F. japonica* and *F. ×bohemica* sites were found. Some species, such as *Aegopodium podagraria* L. and *Symphytum tuberosum* L., were quite frequent in each type of plot. The cover of necromass affects similarly the cover of *F. japonica* in spring but in summer other species are associated with it, such as *Calystegia sepium* (L.) R. Br., *Rubus caesius* L., *Aegopodium podagraria* and *Solidago canadensis* L.

Discussion

Environmental requirements of *Fallopia* taxa and accompanying vascular plant species

In the present study we aimed, among other objectives, to examine soil variables diversity within habitats invaded by *Fallopia* taxa in two similar rivers. In contradiction to other studies (e.g. [36,37]), where selected sites were more variable, the results revealed that sites located along the two rivers hardly differed in the studied soil parameters. Thus, it can be inferred that the sites did not affect the results, and permitted analyses across the two rivers. Previous studies (e.g. [38–44]) demonstrated that in Poland the most frequently invaded habitats and the most favourable conditions (in terms of size of populations and morphometric traits) for species of *Fallopia* genus are riparian biotopes. It can be expected that the soil data obtained exhibited suitable conditions for particular *Fallopia* taxa. In our study it was revealed that pH in soils in the river valleys were estimated at ca. 6.5., whereas in wasteland in Belgium it varied between 4.9 to 7.4 [36]. Also Rahmonov et al. [45] showed that sites invaded by *F. japonica* are very diverse in pH, from 4.0 to 7.5.

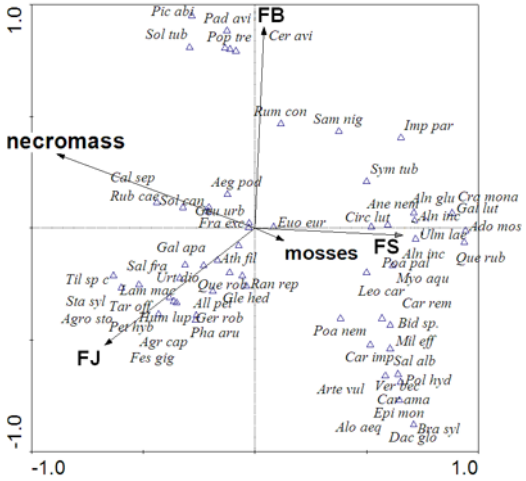

Fig. 6 Biplot of field layer species and *Fallopia* taxa, cover of mosses and necromass as predictor variables on the first two CCA axes ($\lambda_1 = 0.54$, $\lambda_2 = 0.43$) in summer. The diagram accounts for 9.2% and 62.4% of variance of cover species data and fitted species data, respectively. The first three letters indicate the genus and species names, respectively.

Tab. 5 The list of resident species significantly associated with groups of plots dominated by *Fallopia* taxa with value of IndVal, mean ±*SD* of cover and frequency (in parentheses) in spring.

Taxon	IndVal	FJ	FS	FB	Freq
Fallopia japonica					
Urtica dioica	0.528*	8.1 ±9.0(15)	5(1)	3.0 ±2.8(11)	(18)
Phalaris arundinacea	0.516**	2.3 ±1.9(12)	-	-	(12)
Agrostis capillaris	0.471*	1.8 ±1.7(10)	-	-	(10)
Impatiens glandulifera	0.44	1.0 ±0.0(10)	-	-	(10)
F. sachalinensis					
Poa nemoralis	0.632***	-	3.2 ±3.7(6)	-	(6)
Adoxa moschatellina	0.577***	-	5.2 ±3.2(5)	-	(5)
Alnus incana (A)	0.566***		5.0 ±0.0(6)	5.0 ±0.0(3)	(9)
Gagea lutea	0.544**	1.0 ±0.0(2)	2.6 ±2.2(5)	1.0 ±0.0(2)	(9)
Galeobdolon luteum	0.447**	-	5.4 ±4.5(3)	-	(3)
Ulmus laevis (A)	0.447**	-	5.0 ±0.0(3)	-	(3)
Milium effusum	0.365*	-	5.0 ±0.0(2)	-	(2)
Veronica persica	0.346*	1.0 ±0.0(2)	3.0 ±2.8(5)	-	(7)
F. ×bohemica					
Populus tremula (A)	0.483**	-	-	4.4 ±2.8(7)	(7)
F. japonica + F. sachalinensis					
Ficaria verna	0.76	5.8 ±10.8(28)	26.6 ±20.4(10)	4.8 ±5.7(13)	(51)
Alliaria petiolata	0.562*	1.0 ±0.0(18)	1.0 ±0.0(3)	1.0 ±0.0(2)	(23)
F. sachalinensis + F. ×bohemica					
Salix alba (A)	0.447*	5.0 ±0.0(3)	-	5.0 ±0.0(6)	(9)
Total cover of native plants		16.7 ±21.0	22.4 ±24	41.5 ±35.6	

A – tree layer; C – herb layer. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Tab. 6 The list of resident species significantly associated with groups of plots dominated by *Fallopia* taxa with value of IndVal, mean ±*SD* of cover and frequency (in parentheses) in summer.

Taxon	IndVal	FJ	FS	FB	Freq
Fallopia japonica					
Agrostis capillaris	0.447*	1.9 ±1.4(9)	-	-	(9)
Phalaris arundinacea	0.422*	8.5 ±9.6(8)	-	-	(8)
F. sachalinensis					
Alnus incana A	0.49**	15.0 ±0.0(6)	-	40.0 ±0.0(9)	(15)
Ulmus laevis A	0.447**	-	15.0 ±0.0(3)	-	(3)
Poa nemoralis	0.43**	-	1.4 ±0.6(3)	-	(3)
Bidens sp.	0.422*	-	1.3 ±0.6(3)	1.0 ±0.0(1)	(4)
Adoxa moschatellina	0.365*	-	1.0 ±0.0(2)	-	(2)
Cardamine amara	0.365*	-	3.0 ±2.8(2)	-	(2)
Galeobdolon luteum	0.365*	-	10.0 ±7.0(2)	-	(2)
Salix alba C	0.365*	-	1.0 ±0.0(2)	-	(2)
Veronica beccabunga	0.365*	-	2.0 ±1.4(2)	-	(2)
F. ×bohemica					
Populus tremula A	0.483**	-	-	25.0 ±15.3(7)	(7)
Populus tremula C	0.447**	-	-	2.1 ±1.6(6)	(6)
F. japonica + F. sachalinensis					
Alliaria petiolata	0.58*	5.8 ±5.2(17)	4.0 ±2.0(4)	1.0 ±0.0(4)	(25)
Glechoma hederacea	0.465*	5.9 ±9.5(9)	6.0 ±6.2(4)	-	(13)
F. sachalinensis + F. ×bohemica					
Salix alba A	0.447*	-	15.0 ±0.0(3)	15.0 ±0.0(6)	(9)
Total cover of native plants		24.1 ±33.2	26.3 ±20.6	43.3 ±44.2	

A – tree layer; C – herb layer. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

According to Beerling et al. [16] *F. japonica* can survive very harsh conditions with a pH range of 3.0–8.5. In our study the sites invaded by this species were more constrained by pH in CCA in comparison with *F. ×bohemica* and *F. sachalinensis*. However, pH gradients arranged samples across *F. japonica* plots due to the high variation of species composition of accompanying plants. In spite of the fact that results are generally congruent they should be treated with caution because pH was studied by different methods in the cited studies. As regards nitrogen, in our study we focused on nitrate and ammonium ions, which are the available forms of this chemical element for plants, whereas in the majority of studies (e.g. [36,45]) total nitrogen was analyzed and did not exhibit differences among sites [45]. Sites with a higher content of the two forms of available nitrogen were more associated with *F. ×bohemica* and, most of all, with *F. sachalinensis* but not with *F. japonica*, which partially confirms that the latter species can exist in areas with low available nitrogen [16]. With reference to the above, it can be stated that *F. japonica* is the most tolerant to high nitrogen variation in soil when compared to the remaining knotweed species. Concerning organic carbon, in our study soils were not very rich, as in the Belgium sites [36], but ours were more similar to the results obtained by Rahmonov et al. [45] for *F. japonica*. Furthermore, the concentration of phosphorus in our soils was very variable as in sites in Belgium [36]. The significance of the differences in plots scores (CCA) between the three types of plots showed not only slight differences in environmental requirements by knotweeds but, most of all, differences in the biotopic requirements of co-occurring plant species.

Impact of *Fallopia* complex members on resident plant species

As is well known, knotweeds plants grow markedly during the vegetation season. It has already been shown that from mid-April to June rapid longitudinal growth of stems, even as much as 40 cm per 4 days, takes place [20]. In the temperate conditions of Central Europe, all *Fallopia* taxa quickly build a dense leaf canopy from April to May [27]. Also Marigo and Pautou [46] claim that for *Fallopia* taxa, early seasonal development is typical. Taking into account the negative impact of these species on the co-occurring flora [47,48] it could be expected that this impact would be much higher in summer when compared to spring. Indeed, *Fallopia* plants negatively influenced species richness and total cover of plants, but only in July. The negative relation between the cover of necromass at the beginning of the season and *Fallopia* cover, as well as the decrease in necromass in summer may be the result of the decomposition of fallen leaves during the vegetation season. Litter fall by *Fallopia* spp. (*F. sachalinensis*) was proven to cause a reduction in litter fall by native species, which was possible owing to a decrease in the cover of resident species [49]. Some studies concentrate on the litter decomposition rate in *F. japonica* [50] or chemical composition [49], but few studies focused on litter cover over time or its impact on resident species. It was already mentioned in general that the accumulation of leaf and stem litter, as well as a canopy that blocks light [16], are mechanisms which contribute to the displacement of native plants. We expected that the total cover of resident plants would be either lower or similar in summer as an effect of phenological changes and the influence of the knotweeds. However, a significant increase of their cover was observed. This demonstrates that the growth of all plants in the riparian habitat runs similarly, and competition among components of ground flora starts later. A higher number of species is associated with the increasing cover of *Fallopia* species in spring than is the case in summer. Thus, it can be concluded that the phenological aspect can bias interspecific interactions; however, in the peak of the vegetation season the impact of knotweeds is markedly negative. The possible mechanisms of impact are shading [27] and the allelopathic effect of phenolic compounds [14] which are released from leaf litter. The concentration of these compounds in soil solution is varied, but the effect of these substances is higher in early spring [51]. Shading, manifested by the high cover of the *Fallopia* canopy which was already mentioned, according to some sources may inhibit the germination of plants. In our case we observed a decrease in the cover of resident plants in the presence of the increasing cover of knotweeds. Our results suggest that the cover of *Fallopia* spp. mainly negatively affects the cover of resident vascular plants through shading and mechanical competition (overgrowing). As regards particular *Fallopia* taxa it turned out that only *F. japonica* and *F. ×bohemica* exerted negative impact on total cover or species richness and the diversity of native plants. In case of *F. sachalinensis* positive relationship both for cumulative cover of all plants and species diversity of natives with increasing cover of this knotweed was observed. This result is in contrast to the findings of others, but it is worthy to mention that we did not compare invaded and uninvaded plots and made no comparison over time. Perhaps under canopy of *F. sachalinensis* some plant species are eliminated but others can benefit from the loss of the eliminated plants. The difference could arise from the fact that *F. sachalinensis* can have a system of growing underground rhizome distinct from that in the other two *Fallopia* taxa, without forming such compact crowns. Nevertheless, within *F. sachalinensis* stands, the cover of native plants is also rather low (Tab. 5). Even if the general pattern, based on literature data, show that *F. sachalinensis* has a negative impact on plants in riparian habitats, we have shown that sometimes in some sites the situation may be different. Positive correlation between giant knotweed and other species within vegetation dominated by this knotweed species does not have to indicate a positive role of this plant on biodiversity because only comparison with adjacent sites can answer this question. Moreover is worth considering the timing of the impact of the invasive plants on the conditions of habitat and the resident species. Presumably the residence time of *Fallopia* taxa in the river valleys examined is similar (certainly their occurrence en mass is confirmed for 15 years). The negative impact on resident riparian plants might be become detectable more rapidly in the case of *F. japonica* and *F. ×bohemica* compared with *F. sachalinensis*. Nevertheless, it is apparent that the three *Fallopia* taxa influence the co-occurring plant composition in a different way or that the effect can be manifested at a different time in relation to the history of invasion.

Species diversity of particular *Fallopia* taxa patches

Studies which are devoted to the relations between *Fallopia* spp. and resident plants species have not usually presented a complete list of accompanying species. However, sometimes there are brief references to the species richness of the coexisting flora. In our study we had a total of 54 resident species, including 46 native plants and 8 alien plants [neophytes: *Echinocystis lobata* (F. Michx.) Torr. & A. Gray, *Impatiens glandulifera*, *I. parviflora* DC., *Solidago canadensis*, *Quercus rubra* L., *Veronica persica* Poir., *Bidens frondosa* L. and a cultivation escapee *Solanum tuberosum* L.] in 30 plots. This is a relatively small number of species, especially in habitats as species-rich as riparian zones. The previous study showed that totally 420 vascular plat species were found to occur in the section of the Soła river valley, 211 in Biała river valley and 160 in Jasienica stream valley [20]. In different types of habitats i.e. urban wastelands in 40 transects a total of 83 species were found [52]. This is a probably consequence of the relatively long residence time of knotweeds in the sites studied in the present investigation. According to Parepa et al. [30] in the initial phase of invasion, i.e. knotweed establishment, shading is the most crucial factor in the exclusion of resident species, but in later stages of invasion allelopathy might play a major role. That experimental study demonstrated that on average the biomass of native species was 20% lower than in plots without knotweeds, but most interesting was that *F. ×bohemica* had the strongest impact on native plants. In our study in part we found significant differences among knotweeds in their impact on resident plants on the basis of value of correlations between cover of *Fallopia* taxa and the other plants (Tab. 3). Also, the lowest number of significantly associated species for *F. ×bohemica* sites can in part confirm the observations of Parepa et al. [30]. As far as the resident species is concerned, some studies have shown that one of the most frequent accompanying species to *Fallopia* spp. is *Urtica dioica* [16,20,22,52]. It is a nitrophilous species, typical for riparian habitats. Others, such as *Phalaris arundinacea*, *Agrostis capillaris* were also reported by Barney et al. [53] and Beerling et al. [16] respectively. Some species which are commonly recorded as frequent associates e.g. *Galium aparine* L., *Geranium robertianum* L., *Aegopodium podagraria* [16,22] were rare in the present study or did not have a preference for any of the *Fallopia* taxa. Bímová et al. [22] concluded that in *Fallopia* stands only three groups of plants are capable of coexisting with knotweeds: clonal ruderal plants, geophytes, and adult trees. Indeed, *Urtica dioica* belongs to the first group. Among the geophytes observed in this study, apart from the most frequent, such as *Adoxa moschatellina* L., *Glechoma hederacea* and the already mentioned *A. podagraria* and *P. arundinacea*, there were also: *Calystegia sepium*, *Gagea lutea* (L.) Ker Gawl., *Allium ursinum* L., *Anemone nemorosa* L., *Circaea lutetiana* L., *Myosoton aquaticum* (L.) Moench, *Petasites hybridus* (L.) Gaertn., B. Mey. & Scherb. and *Symphytum tuberosum* L. These species were more frequently found in *F. sachalinensis* stands. Geophytes can survive due to a shift in phenology; they start the flowering phase before the rapid growth of the knotweeds, including *F. sachalinensis*, but this does not explain why geophytes are more frequent in giant knotweed stands. It is known that geophytes are less competitive than clonal ruderal plants and trees. One of the possible explanations could be a random distribution of plants, both knotweeds and resident species. Then negative or positive interspecific interactions would not be reflected. A second explanation could be a lower competition ability in *F. sachalinensis* or the already mentioned type of growth of this species. The leaves in this species are the largest in terms of leaf area among *Fallopia* spp. [36]. Thus, shading as a limiting factor ought to play the most significant role when compared with the remaining knotweeds. The most plausible explanation for the higher abundance of resident species is a lower ability for allelopathy in *F. sachalinensis*. On the other hand, other studies exhibited opposite patterns. For instance, Hejda et al. [34] demonstrated the greatest impact on species richness in the case of *F. sachalinensis* in comparison to *F. japonica* and *F. ×bohemica*. It is unknown what effect particular knotweeds exert on all native species through allelopathy. One of species negatively affected by *F. sachalinensis* is *Urtica dioica* [14] which in this study is the least frequent in Giant knotweed stands. The third group mentioned by Bímová et al. [22] was trees. In our study some trees were found to co-occur with knotweeds, such as *Populus alba*, *P. tremula*, *Salix alba*, *Ulmus laevis* and *Alnus incana*. Poplars and willow were recorded as coexisting with *F. ×bohemica*. Trees surely were without doubt present before the appearance of knotweeds in these sites, so we could rather state the relationship the other way round, i.e. that the occurrence of knotweeds is associated with the presence of trees. However we do not know the precise history of invasion by *Fallopia* spp. in this area. Nevertheless, it has already been shown that tree seedlings and small saplings can be outcompeted by *Fallopia* spp. [22]. Apart from *Fallopia* taxa a few invasive alien plant species were observed, such as *Echinocystis lobata*, *Impatiens glandulifera*, *Solidago canadensis* which are known to be quite frequent and abundant in riparian habitats in Central Europe [6,40,54]. The presence of these plants might be the result not only of similar biotopic requirements, but the consequence of invasion meltdown, i.e. mutual facilitation of invasion by a group of alien species. Kuebbing et al. [55] showed that there are still not many convincing, empirical studies supporting this concept. In our study, which revealed the frequent co-occurrence of knotweeds with some alien plant species, might be seen as shedding some light on this problem and requires further research.

Conclusions

We found differences in environmental conditions within one type of habitat – riparian zones – which is in contrast to other studies (e.g. [22]), where a wider array of habitats were investigated. These differences, which were obtained within vegetation patches containing knotweeds, in terms of environmental conditions and the species composition of coexisting plants, may be the consequence of two causes. The first cause may indicate various interspecific biotopic requirements, along the pH gradient, and in the content of nitrogen compounds in soil associated with the knotweed taxa. Thus, species associated with particular *Fallopia* taxa

have similar habitat requirements. Alternatively, the second possible cause is that the knotweeds differ in their impact on resident species, which leads to differences in the species composition of the vegetation patches in which they dominate. Obviously, ecological drift sensu Hubbel [56] is also a possible factor explaining the differences in species composition in *Fallopia* spp. vegetation patches. This requires further detailed research. Knowledge of which native plants are more or less affected by particular knotweed taxa could be essential for nature conservation and management in river valleys. In any case, all *Fallopia* spp. have a negative impact on the species cover and species richness of resident plants, and this process is caused both by living plants and the necromass derived from the above ground biomass derived from the knotweeds. Moreover, it has been shown that the impact is intensified during the vegetation season and is strongest in summertime.

Acknowledgments

This project, No. NN 305384738, is financed by the Polish Ministry of Science and Higher Education. Special thanks to Jadwiga Derwisz, Agata Pawliczek, Tomasz Arendarczyk, Zenon Guzik, Sebastian Bzdęga, Jakub Guzik and Aleksander Woźniak for their help during the field work. We are grateful to two anonymous reviewers for their helpful comments. Ian C. Trueman (UK) kindly improved the English.

Authors' contributions

The following declarations about authors' contributions to the research have been made: design of the study: BTG, GW, KB, TN, DC; field research: BTG, TN, GW, KB, KK, MG, DC; analyzing data: DC; writing the manuscript: DC, BTG, GW, KB.

Competing interests

No competing interests have been declared.

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